

Interactions between soil micro-arthropods and endomycorrhizal associations of higher plants

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SUMMARY

- 1 Symbioses between plant roots and mycorrhizal fungi are almost universal in terrestrial plants and have been widely studied in recent years. The effects of these associations on plant growth and nutrient uptake are extensively documented but much less attention has been paid to the way such interactions are influenced by the soil fauna.
- 2 Existing studies of mycorrhiza-fauna interactions, which relate principally to nematodes and ectomycorrhiza, are briefly reviewed and new data presented concerning interactions between Collembola and vesicular-arbuscular mycorrhiza.
- 3 Evidence from both field and laboratory experiments now suggests that the yield and phosphorus uptake of infected plants may be influenced by populations of Collembola, and that Collembola population growth, in turn, is influenced by the presence of mycorrhizal hyphae.
- 4 It is suggested that reductions in the potential yield of mycorrhizal plants are related to grazing of the external mycelium and that such reductions may be induced by naturally occurring population densities of soil animals.

INTRODUCTION

One of the predominant concerns of many mycorrhizal studies has been the stimulatory effect of mycorrhizal fungi on the yield of infected plants, and it is now widely accepted that this phenomenon results from the provision of an increased, and better dispersed, absorbing surface for plant nutrients (Sanders & Sheikh 1983). In nutrient deficient soils roots are typically surrounded by depletion zones (Bieleski 1973; Bhat & Nye 1974) which limit the rate of supply of immobile nutrients, such as phosphate, to the plant root. The external mycelium of mycorrhizal plants extends beyond these depletion zones and is capable of translocating nutrients to the plant over ecologically significant distances (Gray & Gerdemann 1969; Rhodes & Gerdemann 1975). Quantitative aspects of this relationship have been investigated by Bieleski (1973) and Sanders & Tinker (1973) who have shown that the number of hyphal entry points and length of external mycelium are sufficient to account for observed increases in phosphate inflow to infected plants. The enhanced nutrient status of infected plants results in increased yield, improved

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resistance to a range of ecological stresses including drought (Safir, Boyer & Gerdemann 1972; Allen 1982; Nelsen & Safir 1982) and disease (Marx 1972), and may alter the balance of interspecific plant competition (Fitter 1977; Hall 1978).

Much of the evidence for the beneficial effects of mycorrhizas on plant growth has been based on laboratory experiments in which plants are grown in pots of sterilized soil inoculated with mycorrhizal fungi. These experiments have been conducted mainly by botanists and mycologists and, whilst possible interactions with other microflora have often been acknowledged (Marx 1972), the absence of soil fauna in these studies has been largely ignored.

The influence of soil animals on rates of decomposition and nutrient turnover has been considered primarily in terms of substrate modification, dispersal of microbial inoculum and altered microbial competition as a consequence of selective microbivory: selective or differential grazing of soil fungi has been demonstrated in a number of studies involving nematodes (Sutherland & Fortin 1968), mites (Mitchell & Parkinson 1976) and Collembola (McMillan 1976; Visser & Wittaker 1977; Addison & Parkinson 1978; Newell 1980). In many soils mycorrhizal mycelium may constitute a large proportion of the microbial biomass (Hayman 1978) and thus represents a significant potential food source for soil fungivores. Grazing activity which severs or removes mycorrhizal hyphae will be of particular significance to plants in that it diminishes the effective absorbing surface of mycorrhizal root systems and should reduce the beneficial effects of the association.

SOIL FAUNA-MYCORRHIZA INTERACTIONS: A REVIEW

Whilst few studies have explicitly considered the mechanisms of interaction between soil fauna and mycorrhiza, a growing body of evidence suggests that such interactions exist. Early studies document relationships between nematodes and ectomycorrhizal fungi (ECM); more recent work has, in addition, considered associations involving vesicular-arbuscular fungi (VAM) and Collembola.

Zak (1965, 1967) noted the occurrence of root-feeding nematodes and aphids on mycorrhizal roots of *Pseudotsuga menziesii* and Sutherland & Adams (1964, 1966), who noted the migratory, ectoparasitic existence of *Tylenchorhynchus claytoni* (Steiner) and other nematodes on roots of *Pinus resinosa* (Ait.), suggested that the animals may feed on mycorrhizal fungi. Clark (1964) presented circumstantial evidence that a *Deleadenus* species of nematode was responsible for non-establishment of mycorrhizal *Rhododendron* cuttings and postulated direct feeding on the mycelium.

Feeding by an *Aphelenchoides* species on laboratory cultures of *Suillus granulatus* (L. ex Fries) Kuntze has been demonstrated by Riffle (1967). The nematodes caused large reductions in colony diameter and destroyed up to 87% of the cultures. *Aphelenchoides* species have also been shown to suppress mycorrhizal associations between *Suillus granulatus* and *Pinus ponderosa* Laws and have been implicated in the premature death of trees, following prolonged periods of drought (Riffle 1967, 1975). The nematode *Aphelenchus avenae* Bastian has been shown to

feed on seven different species of ectomycorrhizal fungi grown *in vitro* (Sutherland & Fortin 1968). Significant reductions in colony diameter occurred in all cases and the nematode suppressed associations between *S. granulatus* and *Pinus resinosa*, causing a significant reduction in both the number of mycorrhizal root tips and the length of mycorrhizal root, although there was no significant effect on plant weight in the 5-week time span of the experiment.

More recently a number of studies have investigated the relationships between phytopathogenic nematodes and vesicular-arbuscular mycorrhiza (VAM). Contrasting types of interaction have been reported, including both stimulation (Schenck, Kinloch & Dickson 1975; Atilano, Menge & Van Gundy 1981), and depression (Fox & Spasoff 1972; Hussey & Roncadori 1978) of nematode populations by different mycorrhizal endophytes. Schenck, Kinloch & Dickson found an inverse relationship between numbers of mycorrhizal spores and nematode populations in the field, and better growth of nematode populations in pots with mycorrhizal plants than with uninfected plants, but the nature of this interaction was unclear. Reduced sporulation of VAM in response to population of *A. avenae* has also been reported by Salawu & Estey (1979) but the effects of nematode populations on the mycorrhizal stimulation of plant growth, in a range of studies, are not consistent. Suppression of mycorrhizal plant growth has been reported in experiments by Salawu & Estey (1979) and Atilano *et al.* (1981), but in other experiments nematodes only reduced mycorrhizal plant yields at artificially high densities (Hussey & Roncadori 1981) or had no effect at all (Hussey & Roncadori 1978). Clearly it is not possible to generalize about nematode—VAM interactions from observations of individual species combinations and further studies are required.

Despite the growing body of literature relating to selective fungal feeding in mites and Collembola (Usher, Booth & Sparkes 1982) there have been relatively few studies of interactions between these numerous animals and mycorrhizal fungi. Shaw (1983 and p. 333) describes some preliminary feeding choice experiments in which two species of Collembola were offered a range of ectomycorrhizal and saprophytic fungi. *Paxillus involutus* (Fr.) Fr. was significantly preferred to *Marasmius androsaceus* (L. ex Fr.) and both Collembola species significantly avoided *Heboloma crustuliniforme* (Bull. ex St. Amens) Quel., but the effects of grazing on plant growth and nutrient uptake have not yet been assessed. Warnock, Fitter & Usher (1982) examined the influence of the Collembolan *Folsomia candida* Willem var. *distincta* Bagnall on *Allium porrum* L. plants infected with the mycorrhizal endophyte *Glomus fasciculatum* (Thaxter) Gerdemann & Trappe. Plant growth was stimulated by mycorrhizal infection but in the presence of *F. candida* infected plants grew little better than uninfected plants. Phosphate inflow rates to mycorrhizal plants were significantly reduced in the presence of *F. candida* and the authors conclude that these effects are due to grazing of the external hyphae, rendering the mycorrhizal association ineffective. Interactions between VAM fungi and Collembola have been further investigated by Finlay (1983), and some aspects of these relationships are outlined in the following sections.

MATERIALS AND METHODS

Plant growth and mycorrhizal inoculations

Trifolium pratense L. and *Allium porrum* plants were grown in a (1:1 v/v) mixture of clay loam soil and sand which was steam-sterilized at 10·34 N cm⁻² for 1 hour. The resulting mixture had an Olsen extractable P level of 13 µg g⁻¹ and a pH 6·2. Seeds were surface sterilized in a 7% (w/v) sodium hypochlorite solution and germinated aseptically before being transplanted to 9 cm pots. Mycorrhizal inocula were applied as mixtures of sand, spores and infected root fragments and seedlings were infected by placing 10 g of inoculum below the newly emerging root. Plants were grown in growth chambers with a day temperature of 20°C and a night temperature of 15°C; artificial light was supplied for 16 h day⁻¹ and at an irradiance of 40 W m⁻². Bacterial leachings from non-sterile soil were added to all pots and N was supplied at a rate equivalent to 50 kg ha⁻¹.

Collembola culture, extraction and gut content analysis

Two Collembola species, *Onychiurus ambulans* and *Folsomia candida*, were cultured in 5 cm Petri dishes containing a moist charcoal-plaster of Paris (1:9 v/v) substrate. Animals introduced to experimental pots all exceeded 1 mm in length. Collembola were extracted for counting by flotation in water and transferred to 70% ethanol prior to gut content analysis. Animals were cleared in 30% lactic acid at 90°C, the guts were dissected out using fine needles and placed in 0·05% lactophenol blue to stain fungal material. The gut wall was ruptured to allow penetration of the stain and squashed under a cover slip prior to microscopic examination.

Laboratory experiments

In four laboratory experiments different mycorrhizal and non-mycorrhizal treatments were combined factorially with the presence and absence of Collembola at different densities. The mean initial densities (dm⁻³) for the experiments were as follows; Expt A, 33; Expt B, 50; Expt C, 66 and Expt D, 100. Details of the species combinations are summarized in Fig. 1 and full details are given in Finlay (1983). Plants and Collembola were extracted by gentle washing, root length was determined and the dry weights of roots and shoots were recorded. Where soil phosphate was supplemented it was supplied as NaH₂PO₄ at a rate equivalent to 50 kg ha⁻¹. Phosphate content of plant material was estimated by wet-ashing dried material in a triple acid digest (sulphuric/nitric/perchloric: Allen 1974) and developing the phospho-molybdate blue colour in the diluted extract using ascorbic acid.

Field experiment

The field site was a clay loam soil with a mean level of Olsen extractable P of 13 µg g⁻¹ and had been fumigated with methyl bromide 10 months prior to the start

of the experiment to remove indigenous mycorrhizal endophytes. A randomized block design with four treatments was chosen. All plots received 75 kg ha^{-1} N, 100 kg ha^{-1} K and 2 kg m^{-2} of *Glomus occultus* mycorrhizal inoculum. *Trifolium pratense* seed was drilled to a depth of 4 cm with a 15 cm spacing between rows and the site was divided into sixteen plots each measuring $4 \times 4 \text{ m}$. Control plots received no further treatments. Insecticide-treated plots received 'chlorfenvinphos' (diethyl 1-(2',*d*'-dichlorophenyl)-2-chlorovinyl phosphate) granules at two rates, the recommended normal application rate of 4.5 kg ha^{-1} , and a double rate of 9.0 kg ha^{-1} . Rainfall on the second day following application assisted penetration of the insecticide into the soil volume. Fungicide-treated plots received 'Benomyl' (1-butyl-carbamoyl)-2-(benzimidazol carbamic acid, methylester) as a suspension of 50% wettable powder in 4 litres of water for each plot. The fungicide was applied as a soil drench at 1.1 kg ha^{-1} and plots not receiving benomyl received water at an equivalent rate ($2.5 \times 10^3 \text{ l ha}^{-1}$). Harvests were taken at intervals of approximately 20 days, shoot material being sampled from randomly placed 0.25 m^2 quadrats, and root material and soil animals being sampled from soil cores 8 cm in diameter and 15 cm in depth.

RESULTS

Collembola population responses to mycorrhizal endophytes

Final Collembola population densities and the species used in each of the laboratory experiments are displayed in Fig. 1. In three of the experiments (A, B and D)

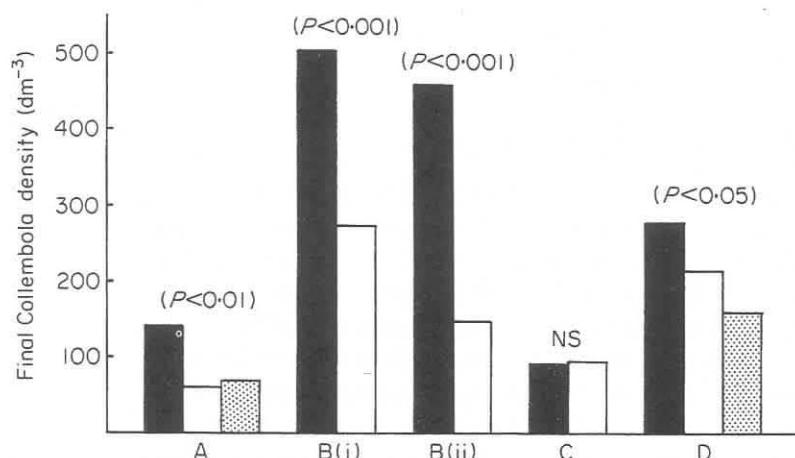


FIG. 1. Final mean Collembola population densities in a range of mycorrhizal (■), non-mycorrhizal (□) and non-mycorrhizal, phosphate supplemented (▨) treatments in four laboratory experiments. Significance levels refer to the effect of mycorrhiza in analyses of variance of ln transformed population data. The plant species was *Allium porrum* in all experiments except D where *Trifolium pratense* was used. The combinations of Collembola and mycorrhizal endophyte were as follows: (A) (*Onychiurus ambulans*, *Glomus tenue*), B (i) (*Folsomia candida*, *Glomus fasciculatum*), B (ii) (*O. ambulans*, *G. fasciculatum*), C (*O. ambulans*, *G. fasciculatum*), D (*O. ambulans*, *G. caledonium*, *G. clarum*, *G. monosporum*, *G. occultum*).

final population densities were significantly higher in mycorrhizal treatment than in non-mycorrhizal ones. In a fourth experiment (C) overall population growth was low and there was no significant difference between mycorrhizal and non-mycorrhizal treatments. A phosphate-supplemented, non-mycorrhizal treatment (P+) was included in experiments A and D to determine whether Collembola population growth was influenced by the larger root systems and enhanced P status of mycorrhizal plants. Phosphate fertilized plants had high shoot P levels and large root systems whose length and weight did not differ significantly from those of mycorrhizal plants, but final Collembola densities in P+ treatments did not differ significantly from non-mycorrhizal controls, indicating that the population growth response was not due to changes in the amount or P-status of root material. The root weight ratios of plants were not reduced by Collembola and microscopic examination of the root systems revealed no evidence of root grazing. In experiment A the endophyte *Glomus tenue* did not significantly increase root weight or length and the increased Collembola population growth in this and other experiments suggests that the animals were responding to the availability of mycorrhizal hyphae as food.

TABLE 1. Gut contents of *Onychiurus ambulans* from Experiment A

Treatment	Number sampled	Number containing:			
		fungal hyphae	fungal spores	organic matter	soil
M + P -	15	10	2	12	15
M - P -	15	1	0	15	15

Collembola gut content analysis

Fifteen Collembola (with visible gut contents) from each of the mycorrhizal and non-mycorrhizal treatments in Experiment A were selected for gut content analysis. The presence or absence of fungal material, organic matter and soil was recorded and these results are displayed in Table 1. Both groups of animals contained organic matter but no fragments were clearly identifiable as root material. All animals with visible gut contents contained soil. Two-thirds of the animals from mycorrhizal pots appeared to have been feeding on fungal hyphae, whereas only one of the animals from the non-mycorrhizal treatments had hyphae in its gut. Two of the animals from mycorrhizal treatments had guts containing fungal spores and the large diameter of these (80–90 µm) suggests they may have been mycorrhizal in origin. Other, non-mycorrhizal, fungi may have been introduced with the soil leachings or the mycorrhizal inoculum but the low incidence of fungal material in the guts of animals from non-mycorrhizal treatments suggests that populations of these fungi were not large or that mycorrhizal hyphae were preferred as food.

Effects of Collembola on mycorrhizal associations

Laboratory experiments

Mycorrhizal infection significantly increased plant growth in all laboratory experiments, but, where final Collembola densities were in excess of 150 dm^{-3} (Expts A, B and D), mycorrhizal stimulation of plant shoot yield was consistently lowered by the presence of Collembola. This phenomenon is demonstrated in Fig. 2, where the significance levels refer to *t* tests between the means of mycorrhizal and non-mycorrhizal treatments at each Collembola density. Collembola had no significant effect on the shoot yield of non-mycorrhizal plants and no effect on the final levels of internal infection in mycorrhizal plants, but the root weight of plants in experiment B was significantly increased by both *O. ambulans* and *F. candida*.

At low animal densities, below 150 individuals dm^{-3} (Expt C), Collembola density had a markedly non-linear effect on the shoot weight, root length and total shoot P content of mycorrhizal plants. The variance due to Collembola density was partitioned into orthogonal polynomial components and significant ($P < 0.01$) quadratic relationships were found in all cases, confirming the non-linear nature of the density effect. The effect is demonstrated for total shoot P in Fig. 3. The beneficial effects of infection were increased with the addition of low to intermediate densities of Collembola but at densities in excess of 100 individuals dm^{-3} these effects appear to decline again. The same trends were observed for shoot weight and root length, with maximum values of these parameters again occurring at an approximate density of 100 individuals dm^{-3} . In all cases non-mycorrhizal plants showed no response to Collembola density.

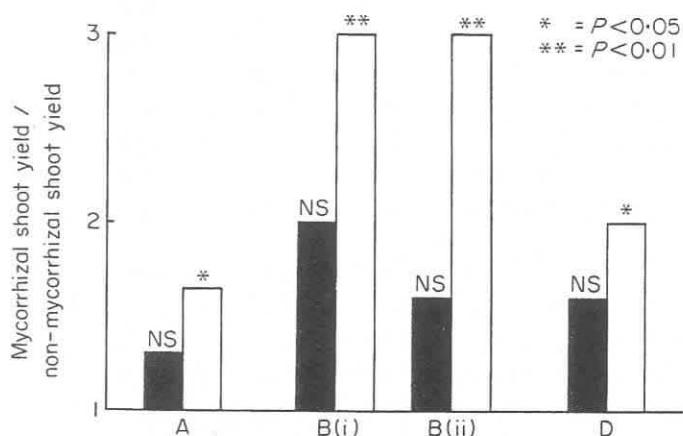


FIG. 2. Mycorrhizal stimulation of shoot yield in a range of laboratory experiments with (■) and without (□) Collembola. Significance levels refers to *t* tests between the means of ln transformed mycorrhizal and non-mycorrhizal treatments at each Collembola density. Species are given in Fig. 1. D refers to *G. caledonium* alone.

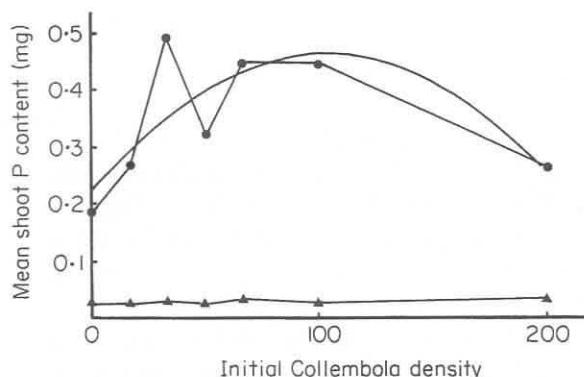


FIG. 3. The relationship between mean shoot P content and initial Collembola density for mycorrhizal (●) and non-mycorrhizal (▲) *Allium porrum* plants grown with seven densities of *Onychiurus ambulans*. The fitted quadratic relationship is shown for mycorrhizal plants.

Field experiment

Applications of the insecticide Chlorgenvinphos resulted in a significant ($P < 0.01$), 80% reduction in the numbers of Collembola extracted compared with control plots. Final populations in treated plots did not exceed 10 individuals 100 cm^{-2} and there was no significant difference between the two rates of application. Numbers of animals in benomyl-treated plots were lower than those in control plots but the difference was not significant, suggesting that the fungicide is of negligible toxicity to Collembola.

Plants treated with benomyl had significantly ($P < 0.05$) lower shoot yields and lower shoot phosphorus levels than control plants, supporting the suggestion by Bailey & Safir (1978) that benomyl adversely affects growth and nutrient uptake by mycorrhizal plants. Soil density was not measured and it is possible that soil compaction may have resulted from the toxicity of the fungicide to earthworms; however, there was no significant reduction in the root length of fungicide-treated plants and soil compaction does not seem a likely explanation of the reduced yield.

Although a non-mycorrhizal control was not available for comparison, the poor growth of fungicide-treated plants suggested that growth was limited by the low soil phosphate levels ($13 \mu\text{g g}^{-1}$) and that the *Glomus occultum* inoculum had had a stimulatory effect on plant growth.

Plants grown in chlorgenvinphos-treated plots, with low Collembola densities, showed significant increases in shoot weight ($P < 0.001$) (Fig. 4), shoot P concentration ($P < 0.01$) and shoot P ($P < 0.001$), suggesting that the higher densities of Collembola in control plots may have had a deleterious effect on the growth of mycorrhizal plants. Collembola density had no apparent effect on root growth and no obvious plant pathogens were observed upon microscopic examination of the roots, which appeared intact and healthy. Soil P (Olsen's extraction) was measured at the second and fifth harvests using samples from the extracted soil cores. Whilst variation between blocks was significant, the pesticide treatments had no significant

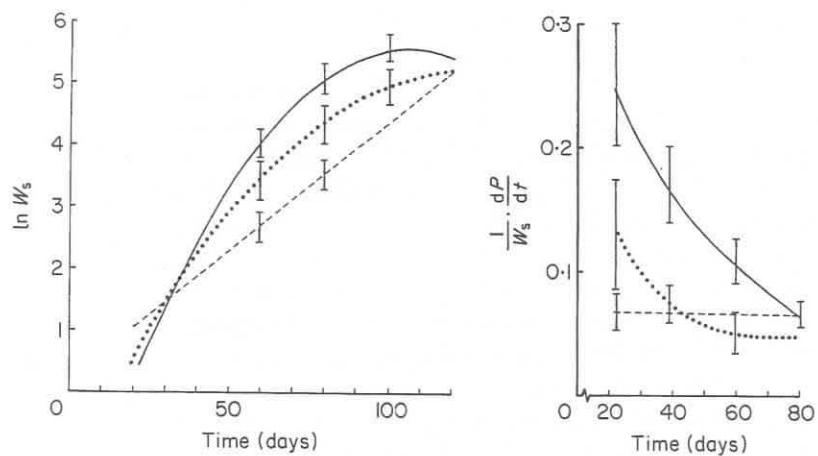


FIG. 4. Changes in (a) mean shoot weight m^{-2} ($\ln W_s$) and (b) rate of shoot phosphate accumulation per unit shoot weight ($1/W_s dP/dt$) in *Trifolium pratense* plants grown in chlorfenvinphos treated (—), control (···) and benomyl-treated (---) field plots. Bars indicate 95% confidence intervals.

effect on extractable soil P, and inclusion of the soil P level as a co-variate in analyses of co-variance did not influence the treatment effects demonstrated above in the analysis of variance. Since estimates of total root length were not available it was not possible to calculate specific uptake rates of phosphorus per unit root length; instead a crude measure of the efficiency of P uptake was calculated as the rate of shoot P accumulation per unit shoot weight. This measure of P accumulation was significantly higher in chlorfenvinphos-treated plants, suggesting a more efficient mycorrhizal association where Collembola densities were low (Fig. 4). Fragments of fungal hyphae were found in three-quarters of the animals whose gut contents were analysed and it is likely that a proportion of this fungal material was mycorrhizal in origin.

DISCUSSION

Soil micro-arthropods and mycorrhizal fungi constitute numerically important components of a wide range of soil ecosystems, and in cases where the mycorrhizal mycelium makes up a large proportion of the microbial biomass, there are likely to be animals that graze these hyphae. Mycorrhizal grazing has been demonstrated in Collembola (Warnock *et al.* 1982) and postulated in the Cryptostigmata (St John & Coleman 1983), but studies of these animals have concentrated on their general role in decomposition processes rather than on any direct influence on plant growth and nutrition.

The results of this study suggest that Collembola demonstrate increased population growth in response to the presence of mycorrhizal hyphae, and that the yield and phosphate uptake of mycorrhizal plants growing in phosphate deficient soil are influenced by different densities of Collembola.

In the laboratory experiments, Collembola populations did not respond to increases in the root system size or P-status of phosphate fertilized plants, but increased in response to the presence of mycorrhizal hyphae even when there was no associated change in root yield. Work by Booth (1979) and Booth & Anderson (1979) has shown that changes in the nitrogen levels of *Coriolus versicolor* and *Hypholoma fasciculare* can influence the fecundity of *Folsomia candida*, but in the experiments reported here nitrate was supplied to all treatments and it seems unlikely that nitrogen supply was limiting population growth.

The experimental results are in broad agreement with those of Warnock *et al.* (1982) in suggesting that grazing of the external mycelium may render the mycorrhizal association less efficient, but additionally suggest that the effects on plant yield and nutrient uptake depend upon the density of Collembola. At low grazing intensities mycorrhizal plant growth is stimulated; the reasons for this are not clear but possibilities include the mobilization of nutrients by animals, selective effects on other microbial populations or dispersal of microbial inoculum. Non-linear responses to grazing intensity have been reported in decomposer systems by Hanlon (1981) and it is possible that low grazing intensities may optimize growth of the external mycelium, whilst at higher Collembola densities the effects of fungal feeding outweigh this or any other beneficial effect.

In the field experiment, the increased yield and phosphate accumulation of plants grown in insecticide-treated plots with reduced Collembola densities were consistent with the effects demonstrated in the laboratory experiments. Interpretation of the results, however, is complicated by consideration of the possible side-effects of the pesticides and the absence of a non-mycorrhizal control in the experimental design, which should ideally have included a factorial combination of mycorrhizal and insecticide treatments.

Benomyl is known to reduce the yield and phosphate uptake of mycorrhizal plants (Bailey & Safir 1978; Boatman *et al.* 1978), whilst it may have a less pronounced effect on other rhizosphere fungi than non-systemic fungicides such as 'captan' (De Bertoldi *et al.* 1977). The reduced yield and phosphate accumulation of fungicide-treated plants suggest that soil phosphate was a major factor limiting plant growth and that growth in other plots had been stimulated by mycorrhizal infection. Whilst benomyl had little or no effect on Collembola density, Chlorfenvinphos caused large reductions in population size consistent with its reported toxicity to Collembola (Tomlin 1975). Chlorfenvinphos is toxic to a wide range of soil animals, including earthworms (Edwards, Thompson & Benyon 1968) and it is possible that large inputs of organic matter may have occurred following the death of soil animals. No change in the soil phosphate level was detected following chlorfenvinphos application however, and available evidence (Hayman, Macdonald & Spokes 1977) suggests that, in soils where P is not limiting, applications of chlorfenvinphos at the normal rate do not stimulate mycorrhizal plant growth whilst applications at higher rates actually decrease plant yield. Applications of the insecticide at normal and ten times normal rates produced an initial inhibition of mycorrhizal infection but infection levels were similar to those in control plants after 19 weeks.

Whilst pesticide-induced changes in microbial populations must not be ruled out as a possible source of influence on plant growth in the field experiment described here, the increased efficiency of phosphate uptake by insecticide treated plants during the initial stages of the experiment (Fig. 4) and the subsequent yield increases in plots with low Collembola densities, together with the apparent absence of root pathogens in control plots, suggest that natural populations of Collembola may limit the efficiency of mycorrhizal associations in the field. These observations are consistent with the beneficial effects of nematicides on mycorrhizal fungi, reported by Ocampo & Hayman (1978) and Bird, Rich & Glover (1974), suggesting that grazing may be of significance in the field, but the extent to which soil fauna-mycorrhiza interactions are purely localized phenomena, influenced by the overdispersion of animal populations and selective feeding on particular mycorrhizal fungi remains to be determined by further experiments.

The beneficial effects of mycorrhiza on plant growth, demonstrated in the laboratory, are frequently less easy to reproduce in the field and the effects of the soil fauna have been largely overlooked as a possible source of variation in these experiments. Whilst frequent reference has been made to the unreality of ignoring mycorrhizal endophytes when considering plant growth, this study emphasizes the need to consider the possible influence of soil animals associated with these endophytes.

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